Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees

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One conceivable outcome of competition for a limited number of pollinators or seed dispersers is the evolution of minimally overlapping flowering or fruiting seasons. In the lower montane forests of Monteverde, Costa Rica, a study of 23 tree species (Lauraceae) that share avian seed dispersers and insect pollinators found little evidence for such phenological character displacement. The distribution of flowering phenologies appeared random but were indistinguishable from a uniform sequence; fruiting seasons were more aggregated and were significantly non-uniform. Nonetheless, ecological competition for seed dispersers apparently does occur because fruit removal rates decline when many species fruit concurrently. Neither intraspecific variance in phenologies nor duration of flowering or fruiting within species was correlated with interspecific competition for dispersers. Final fruit weight at maturity explained only about a quarter of the variance in developmental times between species. The absence of overdispersed phenologies cannot exclude the possibility that competition exists or that phenological character displacement has occurred. Uniformly distributed phenologies have been reported more frequently for flowering than for fruiting. Because flowering plants face reproductive as well as ecological competition, I hypothesize that selection may be stronger for the divergence of flowering times than for fruiting times, especially within guilds of related species.

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Возможный результат конкуренции за ограниченное число опылителей или распространителей семян - эволюция минимально перекрывающихся сезонов цветения или плодоношения. В низкогорных лесах Монтеверде (Коста-Рика) изучение 23 видов деревьев (Lauraceae), которые делят между собой птиц - распространителей семян и насекомых - опылителей, не дало многочисленных доказательств такаго характера фенологического сдвига. Распределение фенологии цветения случайное, но неотличимо от одинаковой последовательности. Сезоны плодоношения более агрегированы и в большей степени неодинаковы. Тем не менее экологическая конкуренция за распространителей семян очевидно имеет место, т. к. скорости изъятия плодов снижаются, если многие виды конкурируют во время плодоношения. Ни внутривидовые различия в фенологии, ни длительность цветения или плодоношения у представителей одного вида, не коррелируют с межвидовой конкуренцией за распространителей. Окончательный вес плодов при созревании объясняет лишь примерно четверть имеющихся различий в периодах развития у разных видов. Отсутствия группового распределения фенологических периодов не может исключить возможность существования конкуренции, либо наличия фенологических смещений. Одинаковая фенология описывается чаще для цветения, нежели для плодоношения. Так как у цветковых растений имеется как репродуктивная, так и экологическая конкуренция, я предполагаю, что отбор может идти более жестко на различия периодов цветения, нежели плодоношения, особенно у групп близкородственных видов.

1. Introduction

Sympatric plants that share the same dispersers and flower or fruit at the same time may reduce each other's fitness, if the plants' reproductive success is limited by pollination or seed dispersal (Robertson 1895, Levin and Anderson 1970, Waser 1978b). Competition between plants for dispersers of pollen or seeds could select for the evolution of staggered and minimally overlapping reproductive schedules. Phenological variation occurs within many plant populations, and the timing of flowering or fruiting is a heritable character on which selection can act (Allard and Hansche 1964, Bergh 1976).

Differences in flowering and fruiting times among sympatric plants have been documented by various researchers, many of whom have interpreted such differences as reflecting adaptations to minimize competition (Tab. 1). In 1977, for example, Stiles reported that plant species were able to avoid competition for pollinators by coevolved, compensatory shifts in phenologies during years when unusual weather patterns disrupted normal, staggered flowering patterns.

The controversy sparked by Stiles' (1977) proposal brought into focus the problem of whether differences in phenology reflect community organization. It also raises the question of what constitutes acceptable evidence to implicate competition as the chief cause of observed phenological patterns (Pole and Rathcke 1979, Gleason 1981, Cole 1981). A uniform (staggered) distribution of flowering or fruiting peaks throughout the growing season has traditionally been accepted as demonstrating character displacement caused by interspecific competition (Snow 1965, Stiles 1977; see references in Tab. 1). However, critics stress that such conclusions are weak unless the study formulates a priori hypotheses, states predictions clearly, and uses statistical tests to compare observed results with explicitly framed null hypotheses (Strong et al. 1979). Recent studies on plant phenologies by Parrish and Bazzaz (1979), Pleasants (1980), Rabinowitz et al. (1981), and Anderson and Shelfhout (1980) have begun to meet these criteria.

This paper, which presents the results of a five-year study of flowering and fruiting seasonality in 23 sympatric tree species in the lower montane forests of Costa Rica, attempts such an approach. The focal species, insect-pollinated and bird-dispersed members of the Lauraceae, were chosen because they represent a guild (Root 1967), a group of species providing similar fruit resources and attracting the same seed dispersers. The trees also share similar floral morphologies and flower visitors. The aim of the study was threefold: 1) to test the prediction that competing trees have uniformly distributed reproductive seasons; 2) to examine possible influence of competition on other aspects of phenologies, such as population synchrony, between-year variability, fruit developmental rates, and seed dormancy; and 3) to evaluate the expectations of the competition

model, the null hypotheses used to test it, and the empirical evidence that has led to its widespread acceptance. I also present a hypothesis about the nature of selection for phenological differences in flowering versus fruiting. The paper emphasizes fruiting rather than flowering patterns, and deals mainly with the question of interspecific competition (rather than physiological cues or constraints) as an ultimate explanation of phenological patterns.

2. Methods

2.1. Study area and methods

The study site, a 15 km² area of lower montane wet and rain forests of Monteverde, Costa Rica (10°18′N, 84°48′W; Holdridge 1967), is composed of undisturbed forests (including the 2700 ha Monteverde Cloud Forest Reserve), small cattle pastures, and woodlots. It sits on relatively nutrient-rich volcanic soil on a gently sloping plateau at an elevation of 1350–1550 m. Westward from the divide, an abrupt moisture gradient caused by the prevailing northwest trade winds creates several distinct habitat types within a distance of 4 km (see Lawton and Dryer 1980). The sharp edge of the plateau and the continental divide which form the boundaries of the study site were selected to circumscribe a discrete area within which plant species interact much more strongly with each other than with species outside the area. The principal birds that feed on lauraceous fruits have their local centers of abundance within the study area and move freely throughout it (Wheelwright 1983, Wheelwright et al. 1984).

Daily maximum and minimum temperatures remain relatively constant year-round at Monteverde (monthly means: T_{max} 19.8°–22.5°C; T_{min} 12.8°–16.2°C [June 1980–June 1981]), with cooler temperatures from December to February. Day length changes by less than an hour over the course of the year. Rainfall is highly seasonal, with most of the ca. 2,500 mm annual precipitation occurring between May and November. Leaf flush, flowering, and fruiting take place in different species every month of the year.

From June through August 1979 I observed flowering and fruiting in six species in the Lauraceae. The following year (June 1980 through July 1981) the study included all 23 bird-dispersed lauraceous species found at Monteverde. At bi-weekly intervals, I censused 286 trees on a 7 km transect along forest trails and pasture edges (median = 10 ind/species; cf. Fournier and Charpentier [1975] and Frankie et al. [1974]). For several rare lauraceous species it was impossible to find more than a few individual trees to monitor. Censuses continued at monthly intervals from August 1981 through July 1982 for a subsample of 3 trees/species. In early March 1982, late February 1983, early August 1983, and early February 1984 I observed all 286 trees. The trees in the 1981-2 subsample, chosen because they had representative phenologies in 1980–1982 and were easily lo-

Tab. 1.
A. Studies of flowering phenologies.

Reference	Plant species	Pollinators	Location	Apparent phenological pattern[2]
Anderson and Schelfhout (1980)	tallgrass prairie plants (77 spp., 24–27/habitat)	insects (wind)	Wisconsin, USA	staggered (or floral morphologies distinct)[1]
Feinsinger (1978)	lower montane forest succesional plants (10 spp.)	hummingbirds	Puntarenas, Costa Rica	staggered
Frankie (1975)	tropical dry forest trees (20 spp.)	medium-large bees	Guanacaste, Costa Rica	staggered
Gentry (1974)	*Arrabidaea* spp. (Bignoniaceae) (5 spp.)	bees	Canal Zone, Panama	staggered
Heinrich (1976)	temperate bog plants (48 spp.)	bumblebees	Maine, USA	staggered
Heinrich (1976)	temperate woodland plants (44 spp.)	bees, flies, wind	Maine, USA	aggregated
Heithaus (1974)	tropical dry forest shrubs and trees (18 spp.) (18 spp.)	hummingbirds butterflies	Guanacaste, Costa Rica	staggered
Heithaus et al. (1975)	tropical dry forest shrubs and trees (13 spp.)	bats	Guanacaste, Costa Rica	staggered
Hilty (1980)	Premontane forest *Miconia* spp. (18 spp.)	insects	Valle, Colombia	staggered[1]
Janzen (1967)	tropical dry forest trees	various	Guanacaste, Costa Rica	aggregated within dry season
Lack (1976)	*Centaurea* spp. (Asteraceae) (2 spp.)	*Apis, Bombus*	England	staggered
Macior (1970)	*Pedicularis* spp. (Scrophulariaceae) (7 spp., 1-3/site)	bumblebees	Colorado, USA	staggered
Mosquin (1971)	temperate successional plants (11 spp., 3–7 sharing pollinators)	insects, wind	Alberta, Canada	staggered (or floral morphologies distinct)
Opler et al. (1975)	tropical dry forest *Cordia* sp.. (Bignoniaceae) (8 spp., 2-3/guild)	birds, mammals, wind	Guanacaste, Costa Rica	staggered
Parrish and Bazzaz (1979)	early and late successional plains spp. (32 spp., 3-17/community)	wind, insects (self-pollinated)	Illinois, USA	aggregated seasonally and diurnally[1]
Pleasants (1980)	Rocky Mountain plants (31 spp., 3-9/guild)	bees	Colorado, USA	staggered within guilds[1]
Pojar (1974)	marsh, bog, subalpine plants (97 spp., 1-20 sharing pollinators)	wind, insects	British Columbia, Canada	staggered

Reference	Plant species	Pollinators	Location	Apparent phenological pattern[2]
Rabinowitz et al. (1981)	prairie plants (82 spp., 5 randomly selected spp./"guild")	wind, insects	Missouri, USA	indistinguishable from random[1]
Rabinowitz et al. (1981)	grasses (11 spp.), composites (14 spp.), legumes (5 spp.)	wind, insects	Missouri, USA	indistinguishable from random[1]
Reader (1975)	bog ericads (5 spp., 3–4/site)	insects	Ontario, Canada	staggered
Schemske et al. (1978)	spring woodland herbs	insects	Illinois, USA	aggregated
Stiles (1977)	tropical wet forest plants (11 spp.)	hummingbirds	Heredia, Costa Rica	staggered
Stiles (1978)	tropical wet forest plants	hummingbirds	Heredia, Costa Rica	staggered
Waser (1978a)	Rocky Mountain wildflowers (2 spp.)	hummingbirds	Colorado, USA	staggered
Wheelwright (present study)	lower montane forest Lauraceae (21 spp.)	insects	Puntarenas, Costa Rica	indistinguishable from random[1]; uniform when weighted by abundance and fecundity[1]

B. Studies of fruiting phenologies.

Reference	Plant species	Seed dispersers	Location	Apparent phenological pattern[2]
Cruz (1981)	montane moist forest shrubs and trees (8 spp.)	birds (bats)	Jamaica, W.	staggered
Heithaus et al. (1975)	tropical dry forest shrubs and trees (13 spp.)	bats (birds)	Guanacaste, Costa Rica	staggered
Hilty (1980)	premontane forest *Miconia* spp. (19 spp.)	birds	Valle, Colombia	staggered[1]
Milton et al. (1982)	*Ficus* spp. (2 spp.)	birds, mammals	Canal Zone, Panama	asynchronous and complementary to the rest of the plant community
Snow (1965)	lower montane forest *Miconia* (22 spp.)	birds	Trinidad, W. I.	staggered
Wheelwright (present study)	lower montane forest Lauraceae (23 spp.)	birds	Puntarenas, Costa Rica	aggregated[1]

1. Statistical analysis of phenologies used.
2. "Staggered" used in the sense of uniformly distributed or minimally overlapping.

cated by a research assistent, had similar phenologies in March 1982 to the larger samples from which they were drawn (Kendall's Coefficient of Concordance: P < 0.001). Phenological data on different individual trees of 12 of the same species (median = 6 ind/species) were collected monthly from September 1978 until June 1980 by W. Haber and G. Frankie (pers. comm.).

At each tree, I used binoculars or a spotting scope to record the intensity of flowering and fruiting (0%, 1–25%, 26–75%, 76–100% of canopy area bearing flowers or fruits). I chose this measure because it was repeatable and provided an estimate of relative crop size and an unambiguous indication of phenological state. Since hundreds of tiny flowers may be produced on a single panicle, with tens of thousands of panicles or fruits borne at heights of up to 30 m, this method was not only the most feasible, but also allowed direct comparisons of phenological peaks between treees of different sizes. I also recorded the proportion of open flowers (0%, 1–25%, 26–75%, 76–100%) and the developmental stage of the most advanced fruits (stages 1–4: recently fertilized, swollen and growing, approximately mature size but still unripe, or ripe). Reproductively mature trees ranged in height from 10–30 m (except for two 2–10 m understory species).

A composite index of population synchrony and mean reproductive condition provided an instantaneous estimate of flower or fruit production by each species and indicated its presumed competitive effect on other species ("competitive index"). The proportion of individuals of a species in flower or fruit was multiplied by their average intensity of flowering or fruiting. For example, 72% of observed *Nectandra davidsoniana* produced ripe fruits in census 5, 64% in census 6, 16% in census 7, and 0% in census 8. Fot those trees that produced ripe fruit, the mean intensity of fruiting (on a scale of 1–4) in censuses 5–8 was 1.5, 1.4, 1.0, and 0, respectively. The competitive index – the product of the two variables – was therefore 1.08, 0.90, 0.16, and 0, respectively.

The date of peak flowering or fruiting for each species was arbitrarily determined as the median of the competitive index distribution (e.g., census 5 for *N. davidsoniana* in the above example). I distinguished periods when at least 20% of the population had open flowers or ripe fruits to avoid giving undue weight to a small proportion of flowering of fruiting individuals, to characterize the "typical" phenology for a species, and to focus on periods where competion was likely to be highest (see Figs 3–4). The most detailed and frequent observations, which also involved the largest sample sizes, were made during 1980–1981. It was an unusually wet year (3274 mm of rainfall), as was the following (> 2900 mm); 1982–1983, in contrast, was quite dry (Campbell pers. comm.). Nonetheless, phenological patterns in 1980–1981 were similar to previous and subsequent years (W. Guindon pers. comm.; cf. Figs 1–2). I tested this by comparing flowering and fruiting intensities for

all 286 individual trees monitored in mid-dry season of 1981, 1982, and 1983. The ranks were similar among years (Kendall's Coefficient of Concordance: flowering, P < 0.001; fruiting, P < 0.02). Therefore, 1980–1981 was considered a representative year in terms of phenology, and all subsequent statistical analyses (nonparametric tests, described in Siegel 1956) were performed on the 1980–1981 censuses.

2.2. The guild

With the exception of one pink-flowered species (*N. sinuata*), all of the Lauraceae at Monteverde produce large displays of small, unspecialized yellow or white flowers visisted chiefly by wasps, bees, and flies but also by many common species of butterflies, bugs, and beetles. At least 15 insect species are frequent visitors at the flowers of *O. bernouliana*. Most lauraceous species have perfect flowers. Among the Lauraceae, pollination biology is best known in *Persea americana* (avocado). Competition for pollinators caused by the simultaneous flowering of other species is known to limit avocado seed set (Gazit 1976, Papademetriou 1976). Although avocados are self-compatible under restrictive conditions, seed set is lower, fruits are smaller, and the incidence of abnormal embryos is higher with self-pollination than with cross-pollination (Gazit 1976, Papademetriou 1976). Some species in the Lauraceae at Monteverde are apparently self-incompatible (e.g., *O. tonduzii*) judging from the fact that flowering individuals spatially or temporally isolated from the rest of the population did not set fruit. Several species are dioecious (*O. bernouliana*, *O. wachenheimii*). Others (e.g., *Phoebe neurophylla*) set large crops even when no other conspecifics appeared to flower nearby, indicating self-compatibility (the same is true for *Umbellularia* [H. G. Baker pers. comm.]). Short-day photoperiods and, to a lesser extent, cold temperatures provide the proximate cues that induce floral initiation in *P. americana* (Buttrose and Alexander 1978).

The fruits of bird-dispersed lauraceous trees at Monteverde are morphologically and nutritionally similar but are distinct from other fruit species. Thus, these species form an ecological guild as well as a taxonomic group. All have single, relatively large seeds (median seed/fruit weight = 0.52) surrounded by a dense pulp. Lauraceous pulp is significantly higher in crude fat, N, and Mg, and lower in total nonstructural carbohydates and Na, than the pulp of nine other plant species important to birds at Monteverde (Mann-Whitney U Test: P < 0.01 [N_a: P < 0.05] Wheelwright et al. 1984). Lauraceous fruits are also distinctly larger than most fruits eaten by birds: mean diameter of the fruits of different lauraceous species ranges from 8 mm to 23 mm (median: 17 mm; the median fruit diameter of 195 co-occurring plant species in families other than the Lauraceae is 9 mm). With the exception of several species in the Myrtaceae (*Eugenia* spp.) and Rutaceae (*Mappia race-*

mosa), none of the ca. 400 bird-dispersed plant species at Monteverde has fruits similar to those of the Lauraceae (several oily, fibrous fruits in the Palmae, eaten occasionally by toucanets, have a large single seed). As predicted, lauraceous species share the same set (4–18 species) of seed dispersers (Wheelwright et al. 1984) and many of the same flower visitors (unpubl. data).

3. Results

3.1. Competition for pollinators and seed dispersers

Within a plant species the first individuals to produce ripe fruits often attracted many fruit-eating birds, but the frequency of visits and the rate of fruit removal dropped as other trees came into fruit. For example, a few trees of *O. tonduzii* began fruiting in late February, 1981, nearly 2 months before the rest of the population. One of these early fruiting trees that I observed for 1–2 h periods at the same time on different mornings during this period attracted 41.0 birds/observation h on 11 April, 34.1 h^{-1} on 17 April, and 28.7 h^{-1} on 25 April. In late April the rest of the plant population as well as trees of many other species began to bear ripe fruit. On 8 May and 16 May, I saw only 0.7 and 0 birds h^{-1}, respectively. The number of seeds regurgitated into seed traps beneath the same tree (a more accurate measure of the total number of fruit-eating birds visiting the tree and of the time they spent in it) fell from 211 in April to 23 in May. The diminishing frequency of visits was apparently not due simply to depletion of the fruit crop or change in fruit preferences by birds, for at the end of May the tree still bore ca. 20,000 fruits and birds continued to feed heavily on *O. tonduzii* fruits in general. Most of the fruits left on the tree ultimately fell to rot under it. Trees that started fruiting in late April–May never drew as many birds as trees that had ripe fruit earlier, when fruit in general was less abundant.

O. bernouliana first ripened fruits in the early dry season, a time of general fruit scarcity at Monteverde. In December and January, fruits were taken from most trees soon (1–9 d) after ripening, but as fruits of other species gradually became more common, removal rates declined, some fruits remaining on the tree for more than three months (unpubl. data). The time between ripening and removal of 628 individually marked fruits on 33 trees was a function of ripening date: December–January < February < March–April (Mann-Whitney U Test: P < 0.001). Many of the fruits that persisted on the trees were attacked by leaf-cutter ants (*Atta* spp.) (22.5% of the original fruit crop), were destroyed by other fruit predators and pathogens (22.6%), or remained uneaten (7.4%). A multiple stepwise regression analysis showed that the date of ripening was the single best predictor of the speed of removal (r^2 = 0.205). Other factors – crop size, individual fruit characteristics, mean fruit characteristics for the tree as a whole – were much less important and collectively explained only an

additional 14.4% of the variance (Wheelwright unpubl.).

Fruits were removed rapidly during times of fruit shortages. In early March, 1982, when fruits were scarce, emerald toucanets (*Aulacorhynchus prasinus*) scoured trees for ripe fruits but had to consume unripe berries of *Hasseltia floribunda, Ficus tuerckheimii,* and *Solanum* spp., or pry open capsules of *Hampea appendiculata* to pick out the unripe arils. During the same period resplendent quetzals (*Pharomachrus mocinno*) ate green *Beilschmiedia* sp. BC fruits, even though they could only partitially digest them (pers. obs.).

Although I did not study pollination in detail for species other than *O. bernouliana,* the huge floral displays of common species (over a million flowers per tree) make it likely that pollinators were also periodically limiting. Competition for pollinators may exist when heavily flowering lauraceous species bloom coincidently (Papademetriou 1976). With such large floral displays per tree, competition for flower visitors could occur within as well as between species, as it does for seed dispersers, but the requirements of cross-pollination and the competitive pressure of other species probably restrict divergence in flowering within species.

3.2. Flowering and fruiting phenologies

Most lauraceous species at Monteverde tended to flower and fruit at approximately the same time each year (Figs 1–2; cf. Methods). The distribution of flowering peaks (number of peaks/census) failed to support the prediction of temporal uniformity. I used a conservative test in which observed phenologies were compared by χ^2 One-sample Tests with expected (mean) values. P-values greater than 0.95 indicate highly uniform distributions, whereas values less than 0.05 indicate significantly non-uniform distributions. The flowering distribution was statistically indistinguishable from the expected distribution (Fig. 1; n = 22 species; P > 0.05). The distribution of fruiting peaks was significantly non-uniform (Fig. 2; n = 23 species; P < 0.01). (Observed phenologies could be tested against various plausible null hypotheses besides temporal uniformity; I use the latter here because of its influence on the development of theory of phenological character displacement [Poole and Rathcke 1979]). Using the method of Poole and Rathcke (1979), which compares the sample variance, P, of the distance between flowering peaks in temporally adjacent species against the expected value, E(P), under the null hypothesis of random peaks, a similar conclusion was reached: flowering peaks in Monteverde's Lauraceae resembled a random distribution whereas fruiting peaks were aggregated (χ One-Sample Tests: P > 0.05, P < 0.001, respectively). The same pattern of seemingly random flowering and statistically aggregated fruiting in the Lauraceae was evident when rainy and dry seasons were considered separately (cf. Stiles 1979, Cole 1981).
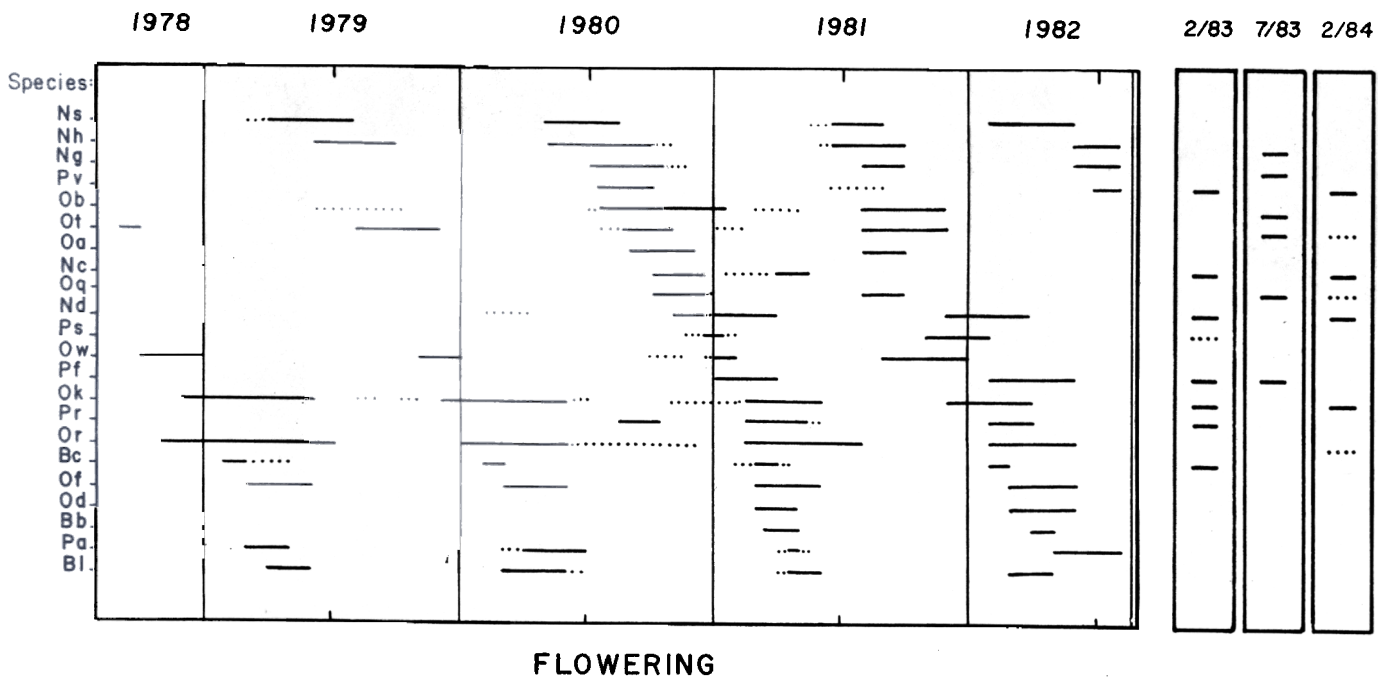
FLOWERING

Fig. 1. Flowering phenologies for 22 species of Lauraceae at Monteverde. Data are incomplete until June 1980. Solid lines represent flowering of at least 20% of the population. Dotted lines record miscellaneous flowering (less than 20% of the population). See Methods and Wheelwright (1982) for a description of sample sizes and explanation of species classifications.

A related prediction was that the number of species flowering or fruiting per census should be about equal throughout the growing season if interspecific competition for dispersers were to be minimized (see Heithaus et al. 1975, Feinsinger 1978). However, the number of tree species flowering during each census did not differ from the expected distribution (Fig. 3; χ^2 One-Sample Test: $P > 0.05$). From two to eight species flowered heavily at any given time. The number of species fruiting per census was significantly uneven (Fig. 4; $P < 0.001$), being highest at the beginning of the rainy season, when over 13 of the 23 species produced ripe fruit
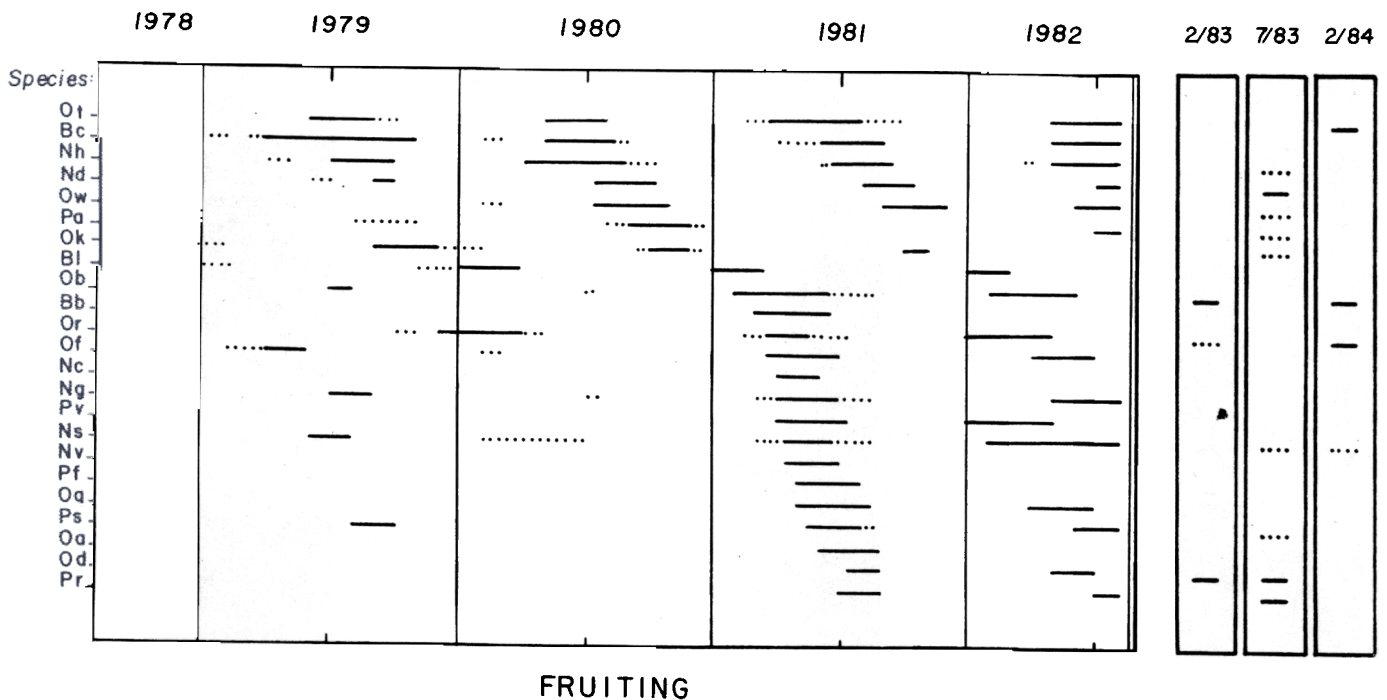

FRUITING

Fig. 2. Fruiting phenologies for 23 species of Lauraceae at Monteverde. Data are incomplete until June 1980. Solid lines represent fruiting of at least 20% of the population. Dotted lines record miscellaneous fruiting (less than 20% of the population).
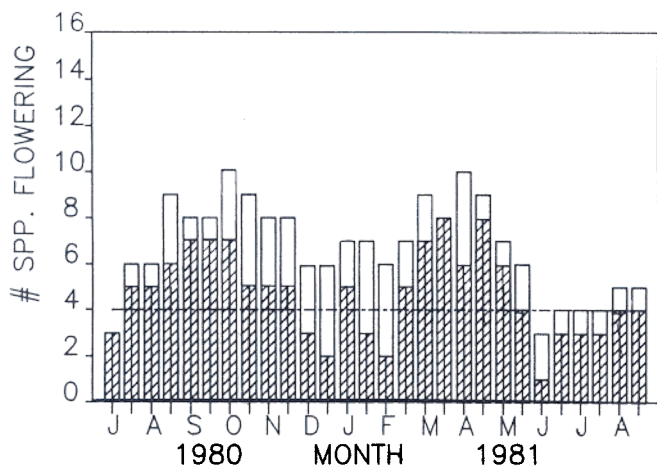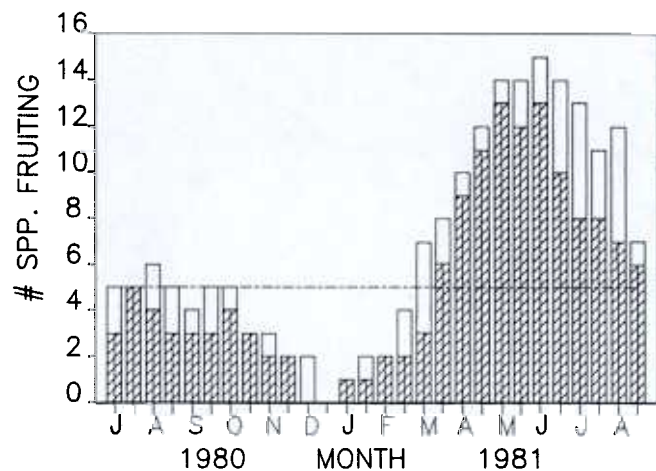
Fig. 3. Numbers of lauraceous species at Monteverde flowering during biweekly censuses from June 1980 through August 1981. Flowering or fruiting seasons for most species extend for 2–4 mo; therefore, each species is represented in several censuses. Hatched bars represent only those species in which at least 20% of the population had open flowers. Open bars include all species in which any individual tree produced flowers. The horizontal line indicates the approximate number of species expected to flower each census if phenologies were uniformly distributed throughout the year.

Fig. 4. Numbers of lauraceous species at Monteverde fruiting during biweekly censuses from June 1980 through August 1981. Hatched bars represent only those species in which at least 20% of the population had ripe fruits. Open bars include all species in which any individual tree produced fruits. The horizontal line indicates the approximate number of species excepted to fruit during each census if phenologies were uniformly distributed throughout the year.

simultaneously. In early dry season, in contrast, fewer than 3 species produced fruit. If the time of seed germination rather than fruit ripening is considered, fruiting phenologies were even more clumped (Fig. 5). The seeds of about two-thirds of lauraceous species germinated within the first 2.5 months of the rainy season (cf. Garwood 1983).

In the tests described above, each species was implicitly given equal weight. But plant species differ in abundance, fecundity, and nectar or fruit quality; they exert unequal competitive effects on other species. Ideally, to test coevolution of reproductive phenologies one should weight each species by its historical abundance and mean annual production of flower or fruit in order to estimate its competitive effect. Lacking such information, I weighted each species according to the product of its current abundance (1–4: rare, uncommon, common, or abundant) and mean biomass of fruit produced per individual (1–4: < 1 kg, 1–10 kg, 10–100 kg, or > 100 kg). Thus, $O.$ sp. OD, a rare, small plant (1×1), was given a competitive weight one-sixteenth that of $O.$ tonduzii, an abundant, highly fecund plant (4×4). In this preliminary analysis, the weighted number of species flowering and fruiting per census was significantly non-uniform (χ^2 One-sample Test: P < 0.02 and p < 0.001, respectively). Note that even weighting
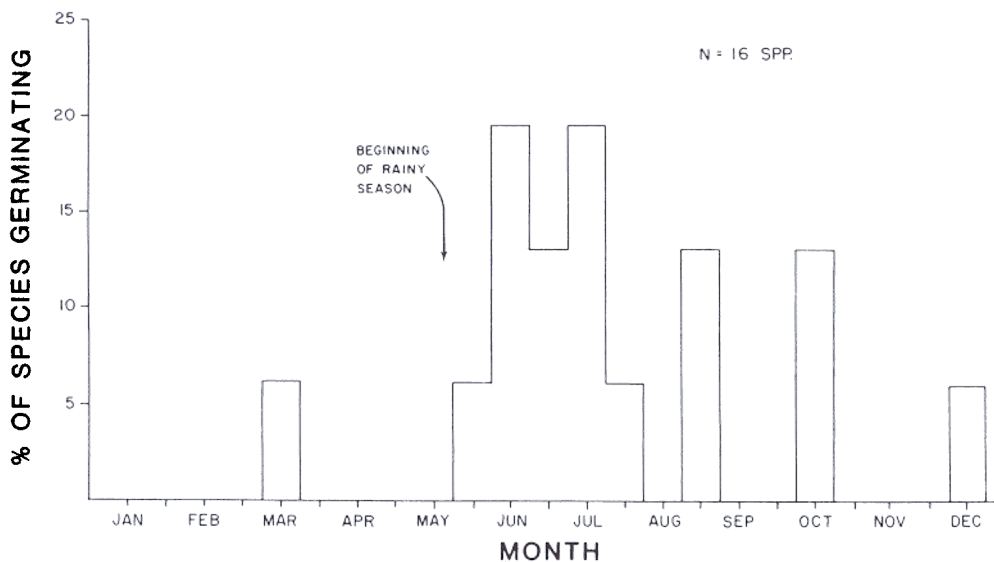

Fig. 5. Distribution of peak germination dates (peak of fruiting plus duration of dormancy) for 16 lauraceous species at Monteverde.

plant species according to their resource production does not necessarily reflect the level of competition they exert on other species because "constancy" of pollinators (Levin and Anderson 1970) or preferences of seed dispersers must also be considered.

I compared phenologies of groups of species within the guild to test the prediction that species sharing the same habitat or producing similarly sized fruits overlap more in their use of seed dispersers and therefore face greater selection to diverge in the timing of fruiting than members of the guild as a whole. However, fruiting phenologies are even more aggregated within habitats (cf. Fig. 1 in Wheelwright 1983). Fruiting phenologies are also clumped within fruit size classes.

Competition for dispersers is unlikely to be restricted to interactions within a guild; it should be affected also by flowering or fruiting seasons within the plant community as a whole. Preliminary phenological analyses for the entire plant community at Monteverde (Haber and Frankie, pers. comm.) indicate that the number of species flowering each month is relatively uniform year-round, with slight peaks in April, May, and October. Fruiting peaks occur in February, May, and September–November. There is no trend towards complementarity for flowering seasons within the Lauraceae and only a slight trend for fruiting seasons (Figs 3–4). In any case, it would be unwarranted without further evidence to interpret such a pattern as community organization due to competition (contra Milton et al. 1982).

3.3. Other phenological patterns

For each species I compared variation within the population in both the timing and the duration of flowering and fruiting against the degree of interspecific competition (estimated by the number of other lauraceous species flowering or fruiting during a species's peak flowering or fruiting period). Other things being equal, natural selection should lead to increased variation in a character (such as phenology) exposed to intraspecific competition (MacArthur 1972). Thus, when interspecific competition is relaxed, one might predict greater phenological variability within populations flowering or fruiting at such times, as well as an increase in the mean duration of flowering or fruiting (cf. Gleason 1981). The sample variance $(nS^2/(n-1))$ of the census number when each individual within a population initiated flowering or fruiting provided a measure of phenological variance for each species. Interspecific competition (as measured here) proved not to be correlated with variation in the onset of flowering or fruiting. The number of simultaneously flowering or fruiting species was also not correlated with the duration of flowering or fruiting for a given species, indicating that the length of neither flowering nor fruiting seasons was abbreviated when competition for dispersers increased (Spearman Rank Correlation: $P > 0.05$ for both tests).

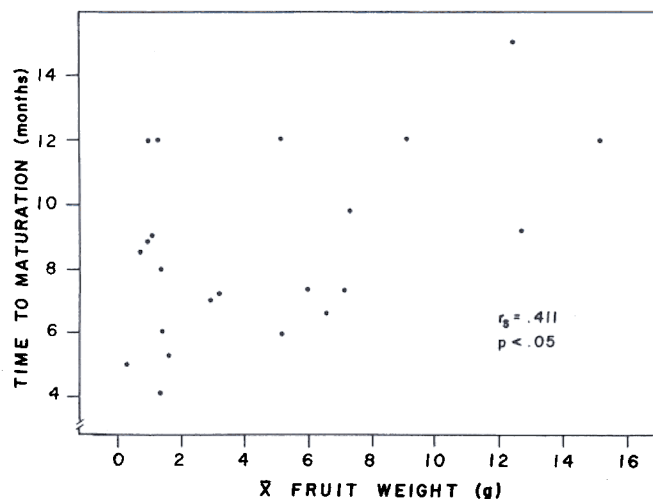The duration of the flowering season within species

Fig. 6. Mean ripe fruit weight versus mean developmental time (period between first open flower and first ripe fruit within individual trees) in 22 lauraceous species at Monteverde.

was not correlated with the duration of the fruiting season in the same species (Spearman Rank Correlation: $P > 0.05$). Thus, fruits produced from flowers opening at the same time developed at different rates, as is known in *P. americana* (C. Campbell pers. comm.). Species in two genera in particular (*Beilschmiedia* and *Phoebe*) have very brief flowering periods and prolonged fruiting periods. Unaccountably, there was a significant negative correlation between population variance in flowering versus fruiting phenology (Spearman Rank Correlation: $r_s = -0.634$; $P < 0.01$): when individuals within a species flowered asynchronously, they tended to fruit synchronously, and vice versa.

Developmental time (mean time between the first open flower and first ripe fruit for all individuals within a population) and mean mature fruit weight were significantly correlated (Fig. 6; Spearman Rank Correlation: $r_s = 0.411$, $P < 0.05$). Yet only about a quarter of the variability in developmental time (least squares regression: $r^2 = 0.240$) was explained by fruit weight. The species with the largest fruit (*B.* sp. BC, 15.2 g) required about the same time (1 yr) to mature its fruits as one of the smallest fruits in the Lauraceae (*O.* sp. RP, 1.1 g). While the timing of flowering phenologies is almost certainly influenced by selection on the timing of fruiting, and vice versa, the wide variance in Fig. 6 belies a tight coupling between flowering and fruiting times. I tested the hypothesis that fruits of different lauraceous species develop at a similar rate until reaching mature size and then simply delay further development until conditions are appropriate to ripen. The time between flowering and the attainment of mature fruit size (but not ripeness) was less closely correlated with fruit size than the time between flowering and fruit ripening (Spearman Rank Correlation: $r_s = 0.180$; $P > 0.05$), which further suggests either relative independence between the timing of flowering and fruiting (cf. Hilty 1980), or distinct

patterns of fruit development in different species within the same plant family.

4. Discussion

4.1. Competition, coevolution, and character displacement

The central question of this paper has been whether directional selection due to interspecific competition for dispersers has been intense enough to counteract opposing selection on phenologies and constant enough to maintain uniformly distributed phenologies. Merely displaying a series of flowering or fruiting phenologies sequentially gives an initial impression of an orderly temporal organization (Figs 1–2; Tab. 1; Poole and Rathcke 1979), but does not answer the question whether reproductive phenologies are organized to minimize overlap.

Neither flowering nor fruiting seasons within the Lauraceae at Monteverde were distinctly uniformly distributed throughout the growing season. Neither were the number of species flowering or fruiting during each census interval uniform, even when species abundances and resource production were considered. Other predictions based on competition for dispersers (intrapopulation variation in phenology, duration of reproductive seasons) did not support the hypothesis of competition-caused temporal organization of flowering or fruiting within the guild. Interestingly, one cannot conclude from this that competition does not exist or that character displacement has not occurred. In fact, competition for dispersers almost certainly does occur at certain times, as shown above (see also Leck [1971], Heithaus et al. [1975], Denslow and Moermond [1982], and Thompson and Willson [1978]). Synchronously fruiting lauraceous trees at Monteverde compete for seed dispersers, in the sense that fruits from any one tree are removed more slowly and face a higher risk of seed mortality when other trees simultaneously produce abundant fruits (pers. obs.). Demonstrating competition-induced character displacement is a problem, but the problem is not solved simply by showing the existence of evenly spaced phenologies. The data presented here cannot rule out less extreme temporal divergence in phenologies due to interspecific competition or character displacements along other resource axes (Parrish and Bazzaz 1979).

Observed flowering or fruiting patterns could be the result of causes other than competition, or traits that are adaptive elsewhere in the plants' range (Snow 1965, Janzen 1980). For example, bird-dispersed Lauraceae in Trinidad, which lies at the same latitude as Monteverde, show a peak in number of species fruiting at about the same time (April–June: Snow [1965]). In northern Australia, most Lauraceae also fruit during the dry season, although somewhat earlier (Crome 1975). Flowering times could be determined by fruiting times, or vice versa, although the relatively low correlation between developmental time and mature fruit weight in the Lau-

raceae suggests appreciable flexibility in the relative timing of flowering and fruiting.

Predation on fruits or seeds could be a selective force on the timing of fruiting in the Lauraceae (Smythe 1970, Augspurger 1981). Little is currently known about the annual activity of predators on lauraceous seeds or about seasonal differences in other potential selective forces, such as competition for space among seedlings or the availability of light gaps.

Environmental factors have been only briefly considered in this paper, although they represent a proximate constraint on the timing of flowering and fruiting in many plant species (Opler et al. 1976 and references therein). Most lauraceous species at Monteverde fruit around the onset of the rainy season (Figs 1, 4). Large seeds, such as those of the Lauraceae, are especially prone to desiccation (Baker 1972) and die quickly when deposited during droughts in exposed areas (pers. obs). The simplest hypothesis for fruiting phenologies in the Lauraceae of Monteverde is that fruits ripen so that seeds will be dispersed when physical conditions are most favorable for germination and seedling establishment (cf. Leck 1970, Frankie et al. 1974, Medway 1972). Seasonal differences in climate and photoperiod at Monteverde are distinct and predictable enough that they could be used by plants as reliable proximate cues for the initiation of reproductive events. For example, in less seasonal forests, environmental cues are less pronounced and cyclic phenological patterns less evident (Koelmeyer 1959, Putz 1979, Hilty 1980). Almost all of the Lauraceae at Monteverde investigated have relatively rapid germination (2–12 wk; median = 6.5), so seed dormancy is apparently not an option. The single exception, *O. wachenheimii*, fruits in August–October and has an eight-month dormancy period; seeds germinate relatively synchronously with the onset of the rainy season. Even if lauraceous seeds were capable of prolonged dormancy, predation is so severe (more than 95% within several days of dispersal in some habitats: Wheelwright unpubl.) that few would survive until conditions improved (cf. Garwood 1983).

4.2. A hypothesis on flowering versus fruiting phenologies

Many more studies have claimed uniformity in flowering phenologies than in fruiting phenologies (Tab. 1). Are flowering phenologies simply studied more commonly than fruiting phenologies, or is uniformity actually more common for flowering times? Although the former is probably true, this study implies greater uniformity in flowering than in fruiting within a plant guild. Hilty (1980) also found flowering to be less seasonal than fruiting in a tropical premontane forest in one of the few other studies to examine flowering and fruiting in the same species (see also Heithaus et al. [1975], Frankie et al. [1974]). Such results suggest that selection pressure among co-occurring plant species is greater for temporal divergence in flowering than in fruiting, or

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that there are fewer constraints on the timing of flowering.

Selection for phenological divergence due to competition for disperser visits should be similar for both flowering and fruiting, but in other respects reproductive penalties are likely to be greater for simultaneous flowering than for simultaneous fruiting. Stigma or stylar blocking is one form of interspecific interference that occurs only when two or more species flower coincidently; seed set may suffer as a result (Waser 1978b). Stigma clogging has no analogue in fruiting. Another cost of simultaneous flowering is lost pollen. To the extent that concurrently flowering individuals of a different species interfere with sequential pollinator movements between plants of the same species, pollination success declines. In contrast, it may actually be advantageous for plants when seed dispersers move to (and drop seeds under) plants of different species, where there are fewer seed predators and greater opportunities for establishment (Wheelwright and Orians 1982). Wasted reproductive effort could also select for divergence in flowering times. Foreign pollen may result in fertilization of ovules. If the resulting hybrids have reduced fitness, the energy and nutrients invested in them by the plant may be unavailable for more viable offspring.

Counterselection against temporal divergence may also be less in flowering than fruiting. While the developing embryo is still attached to the parent plant, it is largely protected from the environment. Its water, nutrients, chemical defenses, and most of its energy are provided by the plant. Theoretically, embryo development could proceed any time the parent is physiologically active; if the growing season extends year-round, flowering should be able to occur at any time pollinators are present. In contrast, the dispersed seed and seedling, independent from the parent plant, are more directly affected by the abiotic and biotic environment. Unless the seed or seedlings can survive desiccation, nutrient scarcity, shade and predation until conditions improve, the timing of fruiting may be restricted to certain favorable times of the year.

dence for the evolution of staggered flowering or fruiting due to competition for dispersers is overwhelming in no study. Most involve few sympatric species, only a single season's observations, or a lack of statistical analyses (Tab. 1).

Yet because these results cannot in themselves prove or disprove competition or character displacement, they raise new questions about the validity of using temporal uniformity to demonstrate community organization. An impressive amount of recent work has been dedicated to the statistical analysis of previously gathered phenological data (Poole and Rathcke 1979, Cole 1981, Gleason 1981), while what may be more crucial to our understanding of reproductive timing in plants is the appropriate design and interpretation of future field studies. The idea of temporal divergence in flowering or fruiting may still be valid, but to test it effectively, one should pose a priori predictions, analyze data in several different ways, and use statistical tests to analyze the results. Rather than selecting random sets of species (Rabinowitz et al. 1981), though, one should make use of prior knowledge of the natural history of the plants and study guilds of interacting species (using independent criteria, besides phenology or taxonomy, to define guilds), ideally in both sympatry and allopatry (Lack 1976) and over several years, Where possible, experimental manipulations are especially effective (Augspurger 1981). Above all, one should explore alternative hypotheses (Snow 1965, Putz 1979), consider selection on phenology due to aspects of plant history besides pollination or seed dispersal (Ågren and Fagerström 1980), and construct biologically sensible null hypotheses (Stiles 1979).

Although more attention should be given to constraints imposed by abiotic factors (Hilty 1980), there is nevertheless too much evidence that animals influence the timing of flowering or fruiting to dismiss the importance of biotic interactions in the evolution of reproductive schedules (Bawa and Beach 1981, Thompson and Willson 1979).

5. Conclusion

By cautiously entitling his paper "A possible selective factor..." and by offering alternative hypotheses, Snow (1965) recognized that competition was only one conceivable explanation for fruiting phenologies that were apparently regular (in fact, Gleason [1981] analyzed Snow's data and found fruiting seasons indistinguishable from random). Yet the notion of temporal organization of flowering or fruiting within plant guilds is still popular (cf. Tab. 1), and the same studies are uncritically cited as having demonstrated competition-induced phenological differences. These studies are listed in Tab. 1 not to criticize their shortcomings with the benefit of hindsight but simply to point out that evidence

References

Ågren, G. I., and Fagerström. 1980. Increased or decreased separation of flowering time? The joint effect of competition for space and pollination in plants. – Oikos 35: 161–164.

Allard, R. W. and Hansche, P. E. 1964. Some parameters of population variability and their implications in plant breeding. – Adv. Agron. 16: 281–325.

Anderson, R. C. and Schelfhout, S. 1980. Phenological patterns among tall grass prairie plants and their implications for pollinator competition. – Am. Midl. Nat. 104: 253–263.

Augspurger, C. K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on Hybanthus prunifolius (Violaceae). – Ecology 62: 775–788.

Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. – Ecology 53: 997–1010.

Bawa, K. S. and Beach, J. H. 1981. Evolution of sexual systems in flowering plants. – Ann. Miss. Bot. Gard. 68: 254–274.

Bergh, B. O. 1976. Avocado breeding and selection. – In: Sauls, J. W., Phillips, R. L. and Jackson, L. K. (ed.), Proc. First Int. Tropical Fruit Short Course: the avocado. Inst. Food Agric. Sci., Univ. Florida, Gainesville, FL, pp. 24–33.

Buttrose, N. S. and Aleaander Mc, E. D. 1978. Promotion of floral initiation in Fuerte avocado by low temperature and short daylength. – Scientia Hort. 8: 213–217.

Cole, B. J. 1981. Overlap, regularity, and flowering phenologies. – Am. Nat. 117: 993–997.

Crome, F. H. J. 1975. The ecology of fruit pigeons in tropical northern Queensland. – Aust. Wildl. Res. 2: 155–185.

Cruz, A. 1981. Bird activity and seed dispersal of a montane forest tree (Dunalia arborescens) in Jamaica. – Biotropica 13 (Suppl): 34–44.

Denslow, J. S. and Moermond, T. C. 1982. The effect of accessibility on rates of fruit removal from tropical shrubs: an experimental study. – Oecologia (Berl.) 52: 170–176.

Faegri, K. and Piji van der, L. 1971. The principles of pollination ecology. – Pergamon Press, Oxford.

Feinsinger, P. 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. – Ecol. Monogr. 48: 269–287.

Fournier, L. A. and Charpentier, C. 1975. El tamaño de la muestra y la frecuencia de las observaciones en el estudio de las características fenológicas de los árboles tropicales. – Turrialba 25: 45–48.

Frankie, G. W. 1975. Tropical forest phenology and pollinator-plant coevolution. – In: Gilbert, L. E. and Raven, P. H. (eds.), Coevolution of animals and plants. Univ. Texas Press, Austin, TX.

– , Baker, H. G. and Opler, P. A. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. – J. Ecol. 62: 881–919.

Garwood, N. C. 1983. Seasonal rhythm of seed germination in a semi-deciduous tropical forest. – In Leigh, E., Rand, A. S. and Windsor, D. (ed.), Seasonal rhythms in a tropical forest. – Smithson. Inst. Press, Washington, DC.

Gazit, S. 1976. Pollination and fruit set of avocado. – In: Sauls, J. W., Phillips, R. L. and Jackson, L. K. (ed.), Proc. First. Int. Tropical Fruit Short Course: the avocado. Inst. Food Agric. Sci., Univ. Florida, Gainesville, FL, pp. 88–92.

Gentry, A. H. 1974. Flowering phenology and diversity in tropical Bignoniaceae. – Biotropica 6: 64–68.

Gleason, S. K. 1981. Character displacement in flowering phenologies. – Oecologia (Berl.) 51: 294–295.

Heithaus, E. R. 1974. The role of plant-pollinator interactions in determining community structure. – Ann. Miss. Bot. Gard. 61: 675–691.

– , Fleming, T. H. and Opler, P. A. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. – Ecology 56: 841–854.

Heinrich, B. 1976. Flowering phenologies: bog, woodland, and disturbed habitats. – Ecology 57: 890–899.

Hilty, S. L. 1980. Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. – Biotropica 12: 292–306.

Hocking, B. 1968. Insect-flower associations in the high arctic with special reference to nectar. – Oikos 19: 259–388.

Holdridge, L. 1967. Life zone ecology. – Tropical Science Center Publication, San Jose, Costa Rica.

Howe, H. F. 1980. Nutmeg dispersal by birds. – Science 210: 925–927.

Janzen, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. – Evolution 21: 620–637.

– 1980. When is it coevolution? – Evolution 34: 611–612.

Koelmeyer, K. O. 1959. The periodicity of leaf change and flowering in the principal forest communities of Ceylon. – Ceylon Forester 4: 308–364.

Lack, A. 1976. Competition for pollination and evolution in Centaurea. – New Phytol. 77: 787–792.

Lawton, R. and Dryer, V. 1980. The vegetation of the Monteverde Cloud Forest Reserve. – Brenesia 18: 101–116.

Leck, C. F. 1970. Comments on the seasonality of fruiting in the neotropics. – Am. Nat. 104: 583–584.

– 1971. Overlap in the diet of some neotropical birds. – Living Bird 10: 89–106.

Levin, D. A. and Anderson, W. W. 1970. Competition for pollinators between simultaneously flowering species. – Am. Nat. 104: 455–467.

Linsley, E. G., MacSwain, J. W. and Raven, P. H. 1964. Comparative behavior of bees and Onagraceae. III Oenothera bees of the Mohave Desert, California. – Univ. Publ. Ent. 33: 59–98.

MacArthur, R. H. 1972. Geographical ecology: Patterns in the distribution of species. – Harper and Row, New York.

Macior, L. W. 1970. The pollination ecology of Pedicularis in Colorado. – Am. J. Bot. 57: 716–728.

McKey, D. 1975. Seed dispersal by animals. – In: Gilbert, L. E. and Raven, P. H. (ed.), Coevolution of animals and plants. Univ. Texas, Austin, pp. 155–191.

Medway, L. 1972. Phenology of a tropical rainforest in Malaya. – Biol. J. Linn. Soc. 4: 117–146.

Milton, K., Windsor, D. M., Morrison, D. W. and Estribi, M. A. 1982. Fruiting phenologies of two neotropical Ficus species. – Ecology 63: 752–762.

Mosquin, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. – Oikos 22: 398–402.

Opler, P. A., Frankie, G. W. and Baker, H. G. 1976. Rainfall as a factor in the synchronization, release, and timing of anthesis by tropical trees and shrubs. – J- Biogeogr. 3: 231–236.

Papademetriou, M. K. 1976. Some aspects of the flower behavior, pollination and fruit set of avocado (Persea americana Mill.) in Trinidad. – Yrbook. Calif. Avocado Soc. 106–152.

Parrish, J. A. D. and Bazzaz, F. A. 1979. Difference in pollination niche relationships in early and late successional communities. – Ecology 60: 597–610.

Pleasants, J. M. 1980. Competition for bumblebee pollinators in Rocky Mountain plant communities. – Ecology 61: 1446–1459.

Pojar, J. 1974. Reproductive dynamics of four plant communities of southwestern British Columbia. – Can. J. Bot. 52: 1819–1834.

Poole, R. W. and Rathcke, B. J. 1979. Regularity, randomness and aggregation in flowering phenologies. – Science 203: 470–471.

Putz, F. E. 1979. Aseasonality in Malaysian tree phenology. – Malaysian Forester 42: 1–24.

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Rabinowitz, D., Rapp, J. K., Sork, V. L., Rathcke, B. J., Reese, G. A. and Weaver, J. C. 1981. Phenological properties of wind- and insect-pollinated prairie plants. – Ecology 62: 49–56.

Reader, R. J. 1975. Competitive relationships of some bog ericads for major insect pollinators. – Can. J. Bot. 53: 1300–1305.

Ridley, H. N. 1930. The dispersal of plants throughout the world. – Ashford, Reeve.

Robertson, C. 1895. The philosophy of flower seasons, and the phaenological relations of entomophilous flowers and the anthophilous insect fauna. – Am. Nat. 29: 97–117.

Root, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. – Ecol. Monogr. 37: 317–350.

Schemske, D. W., Willson, M. F., Melampy, M. N., Miller, L. J., Verner, L., Schemske, K. M. and Best, L. 1978. Flowering ecology of some spring woodland herbs. – Ecology 59: 351–366.

Schoener, T. W. 1974. Resource partitioning in ecological communities. – Science 185: 27–39.

Siegel, S. 1956. Nonparametric statistics. – McGraw-Hill, New York.

Smythe, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. – Am. Nat. 104: 25–35.

Snow, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. – Oikos 15: 274–281.

Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. – Ann. Rev. Ecol. Syst. 12: 253–279.

Stiles, F. G. 1977. Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. – Science 198: 1177–1178.

– 1978. Temporal organization of flowering among the hummingbird food plants of a tropical wet forest. – Biotropica 10: 194–210.

– 1979. Reply to Poole and Rathcke. – Science 203: 471.

Strong, D. R., Szyska, L. A. and Simberloff, D. S. 1979. Tests of community-wide character displacement against null hypothesis. – Evolution 33: 897–913.

Thompson, J. N. and Willson, M. F. 1979. Evolution of temperate fruit/bird interactions. – Evolution 33: 973–982.

Waser, N. M. 1978a. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. – Ecology 59: 934–944.

– 1978b. Interspecific pollen transfer and competition between co-occurring plant species. – Oecologia 36: 223–236.

Wheelwright, N. T. 1982. Fruit characteristics and the foraging behavior of tropical fruit-eating birds. Ph. D. Dissertation, Univ. of Washington, Seattle.

– 1983. Fruits and the ecology of Resplendent Quetzals – Auk 100: 286–301.

– and Orians, G. H. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. – Am. Nat. 119: 402–413.

– , Haber, W. A., Murray, K. G. and Guindon, C. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. – Biotropica 16: 173–192.

Wiens, J. A. 1977. On competition and variable environments. – Am. Sci. 65: 590–597.

Willis, E. O. 1966. Competitive exclusion in birds of fruiting trees in Western Colombia. – Auk 83: 479–480.